

**DESCRIPTION OF THE MALE OF *SOSIPPUS PLACIDUS*,
WITH NOTES ON THE SUBFAMILY SOSIPPINAE
(ARANEAE, LYCOSIDAE)**

Petra Sierwald: Department of Zoology, Insects, Field Museum of Natural History,
1400 South Lake Shore Drive, Chicago, Illinois 60605 USA

ABSTRACT. The male of the Florida funnel-web building wolf spider species *Sosippus placidus* Brady 1972 is described and figured for the first time. Analysis of the male palp's morphological structure reveals that *Sosippus* possesses a median apophysis like other members of the Araneoclada, but which of the three additional tegular apophyses is the conductor cannot be determined at present. The study demonstrates that the palea, the putative key apomorphy of the clade Venoniinae-Allocosinae-Pardosinae-Lycosinae requires further morphological analysis. The genus *Porrmosa* is a close relative of the genus *Sosippus* based on shared characters in the male palp. The ontogeny of the female copulatory organs of *Sosippus* agrees with that of other members in the RTA clade. *Hippasella nitida* Mello-Leitão 1944, placed by Capocasale (1990) in the genus *Sosippus*, is not recognized as a congener.

Keywords: *Porrmosa*, lycosid subfamilies, male palp structure

Members of the North American wolf spider genus *Sosippus* Simon 1888 build rather large funnel-shaped capture webs in shrubs and herbaceous vegetation. The webs are strikingly similar to the "typical" agelenid webs. The web-building habit of *Sosippus* and a few other lycosid genera is frequently cited as "unusual" for the hunting spiders, as Lycosidae are often called (e.g., Gertsch 1949: 194). Simon (1898: 322) placed *Sosippus* and some of the other lycosid genera with long posterior spinnerets in the Hippasae (later subfamily Hippasinae), whereas he assigned *Aulonia* C.L. Koch 1848, which also has long posterior spinnerets, to the Lycosae (later subfamily Lycosinae). Roewer (1959: 7) suggested transferring all lycosid genera with long posterior spinnerets to the Hippasinae. Lehtinen & Hippa (1979: 3) argued that the funnel-web is "simply a plesiomorphic character for a wide group of families within the Amaurobiomorpha," rendering the Hippasinae as defined by Roewer polyphyletic. Citing genitalic characters, they placed *Sosippus* in the Lycosinae.

Dondale (1986: 329) introduced the new lycosid subfamily Sosippinae, containing *Sosippus*, "... *Porrmosa* and its relatives," but did not provide a listing of all genera to be included. He also proposed a new subfamily system for the Lycosidae, placing the Sosip-

piniae as sister taxon to the four other subfamilies, the Venoniinae, Allocosinae, Pardosinae and Lycosinae. Groups and nodes of Dondale's subfamily system are supported exclusively by morphological characters of the male palp. Since the Lycosidae is a species-rich family with considerable morphological diversity of the copulatory organs and the sistergroup to the Lycosidae is not yet known, the characters cited by Dondale require further analysis with regard to polarization (e.g., "loss" of terminal apophysis) and homology status. Zyuzin (1985, 1993) proposed a somewhat different subfamily system for the Lycosidae, stressing the importance of characters derived from the copulatory organs as well. He did not discuss Dondale's proposal of the new subfamily Sosippinae.

In the present study, the male of *S. placidus* is described for the first time, and the structural relationships of the sclerites in the genital bulb are analyzed. Comparison with sclerite and apophyses structure in palps of other lycosid groups will establish testable homology hypotheses required for further phylogenetic analyses of the Lycosidae. The ontogeny of the female organs is also illustrated.

Taxonomic history of the genus.—In the first revision of the genus, Brady (1962: 131) placed the then-known North and Central American *Sosippus* species in two groups: one

group with an eastern North American distribution, including *S. floridanus* Simon 1898, *S. mimus* Chamberlin 1924, and *S. texanus* Brady 1962; and the other group with a western and Central American distribution, including *S. californicus* Simon 1898, *S. mexicanus* Simon 1888, *S. michoacanus* Brady 1962, *S. plutonus* Brady 1962, and *S. agalenoides* Banks 1909. In a subsequent study of the eastern North American species (called *floridanus* species group), Brady (1972) described the additional species, *S. janus* and *S. placidus*. The latter species was based on female specimens alone; and its current known distribution is restricted to Highlands County in central Florida, near Lake Placid. Capocasale (1990) transferred the South American *Hippasella nitida* Mello Leitão 1944 to the genus *Sosippus*.

METHODS

During studies in Florida, the author obtained nine juvenile *S. placidus* specimens from Dr. M. Deyrup, who collected them at Archbold Biological Station near Lake Placid at the original type locality. The specimens were reared in the lab; they built capture webs and took prey readily. Three males matured in April 1987. The molted exoskeletons of all specimens were collected. Exoskeleton sections from between the book lungs were removed from the juvenile and subadult females' molts and mounted ventral side up on SEM stubs. The samples were air-dried and sputter-coated. SEM photographs were taken with several different scanning electron microscopes at the Field Museum and at the National Museum of Natural History (Washington, DC). *Sosippus* specimens of other species were borrowed from institutions listed in the acknowledgments. All measurements are in mm.

In 1994, it was suggested that *S. placidus* be placed on the list of endangered and threatened species (U.S. Dept. of the Interior. Federal Register 59(219): 58982), but this proposal was not adopted (U.S. Dept. of the Interior. Federal Register 61(40)).

Sosippus placidus Brady 1972

Figs. 1-9

Sosippus mimus [in part], -Brady 1962: 156, figs. 34, 35.

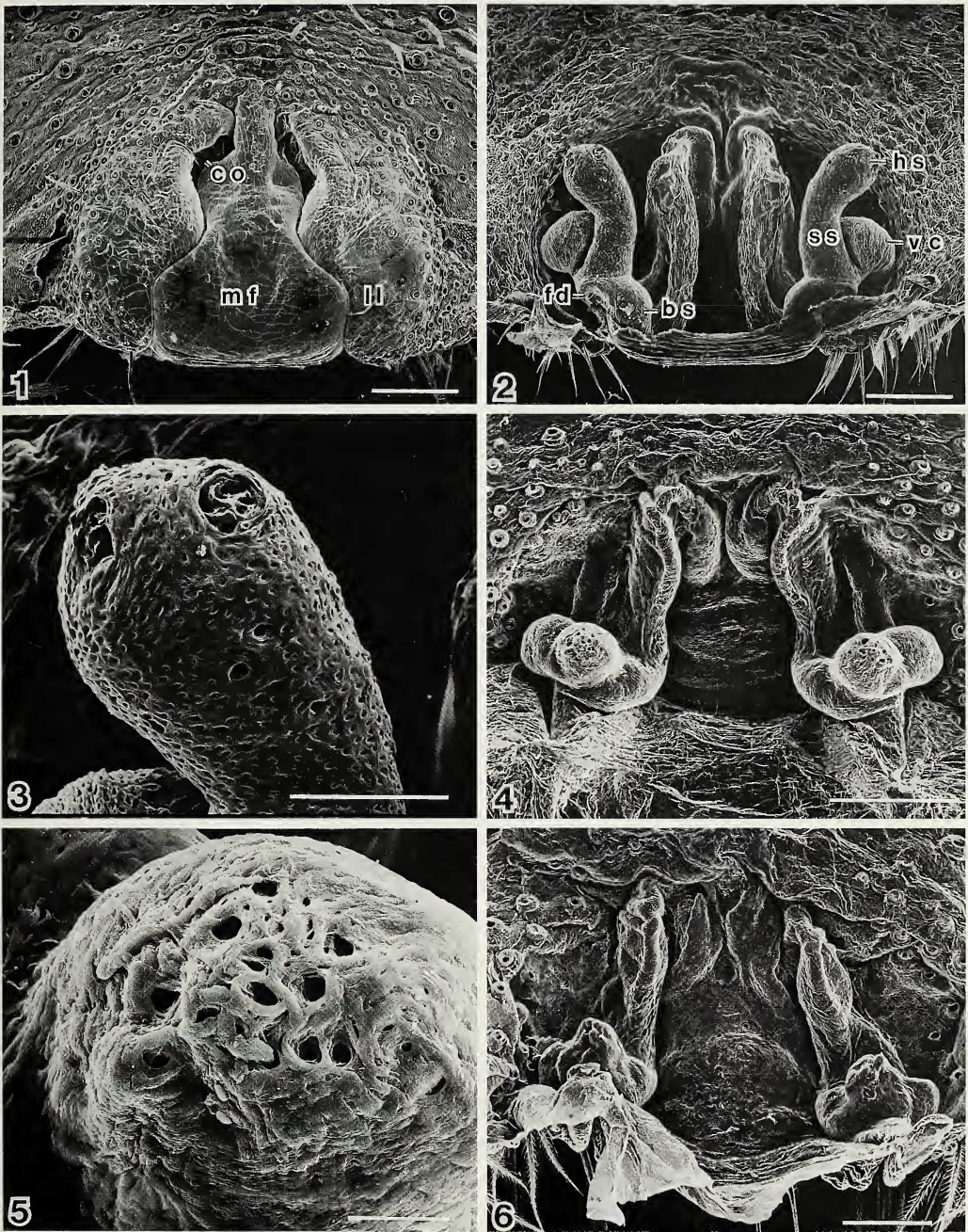
Sosippus placidus Brady 1972: 46, figs. 25-27, 39, map 1. ♀ holotype: USA, Florida, Highlands

County, 6 miles W of Lake Placid, Brady & Tothaker coll.; MCZC. Brignoli 1983: 458.

Diagnosis.—*Sosippus placidus* can be distinguished from all other members of the genus by the bright orange ventral coloration of sternum, legs and abdomen; large adult size (♀ 19-32 mm, ♂ 16-24 mm); and the three retromarginal cheliceral teeth, of which the innermost is twice as large as the other two. *Sosippus texanus* Brady 1962 is very similar to *S. placidus* in body size, number and size ratio of cheliceral teeth and morphology of the copulatory organs, but it lacks the bright orange ventral coloration. Almost the entire middle field of the epigynum (also called septum by other authors) is very broad in *S. texanus* (see Brady 1962, figs. 21, 22), whereas it widens only posteriorly in *S. placidus* (Fig. 1). In the male palp, apophysis *a* is tapered with a round tip in *S. texanus* (see Brady 1962, figs. 37-39), whereas it carries a distinctly swollen tip in *S. placidus* (Fig. 7).

Relationships.—The eastern North American species *S. mimus*, *S. janus*, and *S. floridanus* possess four retromarginal cheliceral teeth (with some individual variation). The remaining species in the genus have three cheliceral teeth; in *S. texanus* and *S. californicus* these have the same size ratio as in *S. placidus* (unknown for the remaining species). Detailed studies into such morphological characters may provide support for the delineation of species groups.

Description.—*Male*: Measurements (3♂): body 16.0-24 long, carapace 6.2-7.5 long, 5.3-7.0 wide; sternum 3.0-4.5 long, 2.1-3.7 wide; labium 0.6-0.9 long, 0.2-0.5 wide. Right leg IV, femur 7.5-10.5 long, patella-tibia 10.0-12.0, metatarsus 10.0-12.5, and tarsus 3.3-6.5; total leg length: 34.0-41.5. Males slightly smaller than females with longer legs than females (see below). Leg formula IV, I-II, III; length: leg IV 34-41.5; legs I and II 30-32; Leg III, 21-25. Spination of legs (see Table 1): spination of femur and patella identical in all species of the genus (with some individual variation); spination of tibia and metatarsus with intraspecific variation especially regarding the dorsal tibial spines on legs III and IV. Color pattern: Carapace orange brown (rust), eye region dark with eyes circled in black; a black thin stripe lining the periphery of the carapace. Chelicerae brownish-



Figures 1-6.—*Sosippus placidus*, female copulatory organs; SEM. 1. External features; *co* = copulatory opening, *ll* = lateral lobe, *mf* = middle field; 2. Internal organs; *bs* = base of the spermatheca, *fd* = fertilization duct, *hs* = head of spermatheca, *ss* = stalk of spermatheca; *vc* = vulval chamber; 3. Head of spermatheca enlarged, showing pores; 4-6. Anlagen of the female copulatory organs, dorsal view, molts. 4. Penultimate instar; 5. Penultimate instar, head of spermatheca enlarged showing pores; 6. Antepenultimate instar. Scale bars: Figs. 1, 2 = 0.2 mm; Figs. 3, 6 = 0.05 mm; Fig. 4 = 0.1 mm; Fig. 5 = 0.001 mm.

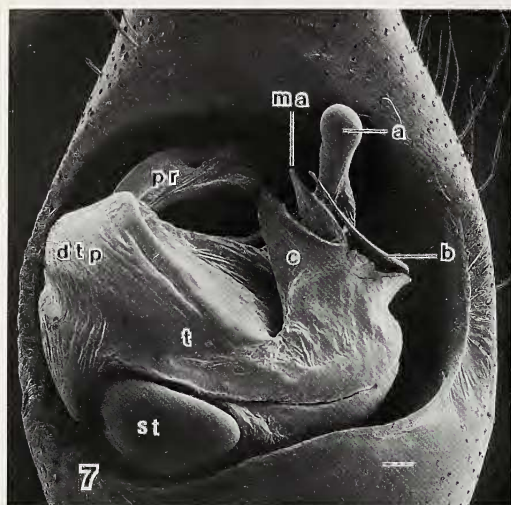


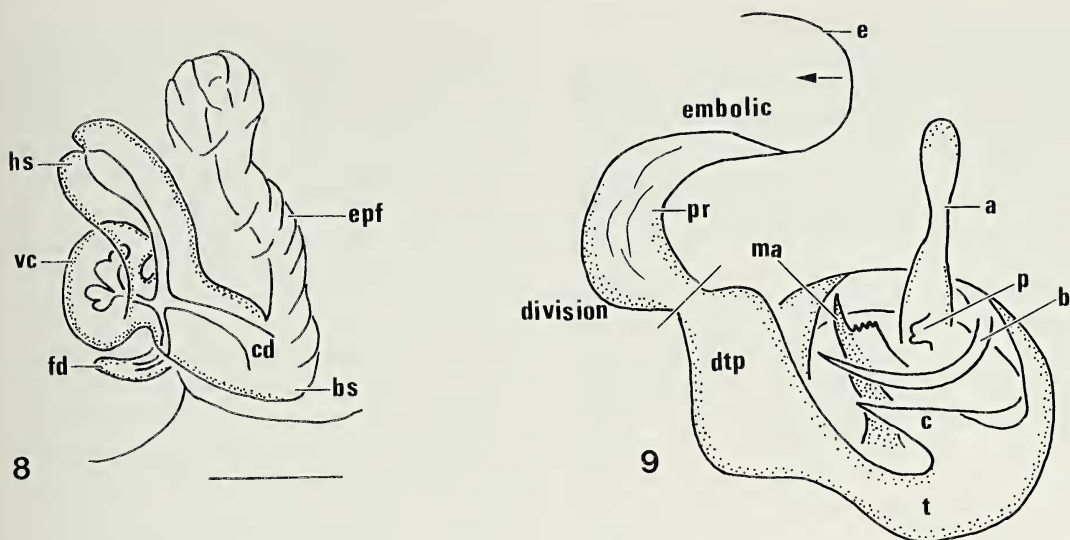
Figure 7.—*Sosippus placidus*, left male palp, ventral view; SEM. Abbreviations: *a*, *b* and *c* = tegular apophyses; *dtp* = distal tegular projection, *ma* = median apophysis, *pr* = palea region, *st* = lunar plate of subtegulum, *t* = tegulum. Scale bar: 0.5 mm.

black; sternum pale orange to yellow (in alcohol); labium and endites darker orange to reddish-black. Ventral surface of abdomen tan to orange, laterally darker orange to red with black hairs; dorsum light brown to tan. Legs brown with alternating light and dark bands; coxae and trochanters bright orange to yellow, covered with white hairs. Palp (Figs. 7, 9): apophysis *a* (labeled conductor by Brady (1962), see discussion below) distinctly swollen and tip sclerotized (Fig. 7).

Female: Measurements (8♀): body 19.0–32.0 long; carapace 6.8–8.4 long, 6.0–7.0 wide; sternum 3.5–4.7 long, 2.4–3.7 wide; labium 0.6–1.1 long, 0.3–0.6 wide. Right leg IV: femur 5.0–8.4 long, patella-tibia 8.4–10.0, metatarsus 4.2–8.7, tarsus 3.3–5.0. Total leg length: 24.0–30.3. Leg formula, spination and color pattern as in male (see also Brady 1972: 47), except for two dorsal rows of five white spots along the axis of the abdomen (see Brady 1972, fig. 39). Epigynum (Fig. 1) with a wide posterior section of the middle field (septum), and large copulatory openings in anterior region of the epigynal folds; internal organs (Figs. 2, 8, and see below) consist of true spermatheca with base, stalk and head, and a kidney-shaped sclerotized chamber (labeled *vc* vulval chamber).

Specimens examined: *Sosippus californicus*: MEXICO: Sonora, San Pedro Bay, 1♀, 17 July 1921, coll. J.C. Chamberlin (paratype of *S. pragmaticus* Chamberlin 1924); CASC. *Sosippus floridanus*: UNITED STATES: Florida, Alachua County, Gainesville, 2♀1♂ (immature), 16 November 1935, coll. W.A. Murrill; MCZC. Alachua County, 1♂, 8 May 1934, coll. A.F. Carr, det. Brady; AMNH. Highland County, Highland Hammock State Park, Sebring, 1♀, 24 March 1938, coll. Gertsch, det. Brady; AMNH. *Sosippus janus*: Florida, Alachua County, NW shore of Lake Lochloosa, 3♀, 10 June 1968, coll. A.R. Brady and J. Toothaker; MCZC. Alachua County, 1♀1♂, 18 April 1935, coll. A.F. Carr; AMNH. *Sosippus mimus*: Florida, Liberty County, Blountstown, 6♂, 17 April 1938, coll. Gertsch; AMNH. Texas, Hidalgo County, Edinburg, 1♀, September–December 1933, coll. Mulaik; MCZC. Florida, Highland County, Lake Placid, 1♀, 1♂ (immature), 1943, coll. M. Cazier, det. Brady; AMNH. Liberty County, Blountstown, 1♂, 4♀ (immature), 17 April 1938, coll. Gertsch, det. Brady; AMNH. *Sosippus placidus*: Florida, Highland County, Lake Placid, Archbold Biological Station, 6♀3♂, September 1986, coll. M. Deyrup; USNM, CASC, FMNH. Highland County, Lake Amiz, 2♀, 25 August 1975, coll. Brach; USNM, MCZC. *Sosippus texanus*: Texas, Aransas County, Goose Island State Park, 2♀1♂, 15 June 1961, coll. A.R. Brady; MCZC. Hidalgo County, Edinburg, 1♀, September–December 1933, coll. Gertsch, det. Brady; AMNH. *Porrmosa harknessi* (Chamberlin 1916): PERU, Huadquina 5000 ft, 1♂ holotype, July 1911, Yale Peruvian Expedition; MCZC.

Structure and ontogeny of the *Sosippus* vulva.—The female copulatory organs develop via the formation of paired longitudinal invaginations, termed epigynal folds (*epf*), above the epigastric furrow (Figs. 4, 6). Such folds have been observed in several families in the RTA-clade *sensu* Coddington & Levi (1991) (see Sadana 1972; Lachmuth et al. 1985; Sierwald 1989). The internal female organs (Fig. 2) consist of the true, tri-partite spermatheca with base (*bs*), stalk (*ss*) and head (*hs*) as identified for many Lycosoidea (Sierwald 1989; Griswold 1993). The head of the true spermatheca is clearly recognizable by its pores on the top (Fig. 3). Attached to the base of the spermatheca is a kidney-shaped, sclerotized chamber (*vc*, Fig. 2; labeled *B* by Brady 1962, fig. 20), whose anterior tip lies ventrally of the stalk of the spermatheca (Fig. 8). The copulatory opening is formed by the elongated epigynal folds; the internal sections of the folds are membranous



Figures 8, 9.—Schematic drawings of copulatory organs. Stippling indicates sclerotized areas, lines indicate membranous sections; 8. Trajectory of ducts in vulva, schematic; abbreviations as in Fig. 2, *cd* = copulatory duct; 9. Sclerites of left *Sosippus* genital bulb in ventral view, schematic; *a*, *b*, *c* = tegular apophyses; *p* = protuberance of apophysis *a*; *dtp* = distal tegular projection, *e* = embolus, *ma* = median apophysis, *pr* = palea region, *t* = tegulum. Embolic division tilted out of original position, arrow indicates direction of tilt.

and rather wide, thus resulting in a wide copulatory opening (Fig. 1). The sclerotized base of the spermatheca is attached to the posterior end of the epigynal folds, enclosing the copulatory duct (Figs. 2, 8). The copulatory duct branches into the duct of the spermathecal stalk and the duct leading into the kidney-

shaped vulval chamber. The fertilization duct branches off from the vulval chamber duct.

Antepenultimate and penultimate molts (Figs. 4–6) possess anlagen of the female organs. The ontogeny of these organs follows the same pattern observed in various Pisauridae (Sierwald 1989) and corresponds closely

Table 1.—Leg spination in *Sosippus placidus*. Abbreviations: 1 = spine normal length, i = short spine, [] = common variation, [variations] = different variations common in this location.

	Femur	Patella	Tibia	Metatarsus
Leg I dorsal	11 i	0	0	0
Prolateral	11	1	1 1	1 i [variations]
Retrolateral	iii	1	1 1 [0]	1 i [variations]
Ventral	0	0	[1]11 11 ii	11 11 i
Leg II dorsal	11 i	0	0 [1 1]	0
Prolateral	11	1	1 1	1 i [variations]
Retrolateral	iii	1	1 1 [0]	1 i [variations]
Ventral	0	0	11 11 ii	11 11 i
Leg III dorsal	11 i	0	0 [1 1]	0 ii
Prolateral	11	1	1 1	1 1 i
Retrolateral	iii	1	1 1	1 1 i
Ventral	0	0	11 11 ii	11 11 i
Leg IV dorsal	11 i	0	0 [1 1]	0 ii
Prolateral	11	1	1 1	1 1 i
Retrolateral	i	1	1 1	1 1 i
Ventral	0	0	11 11 ii	11 11 i

to the one observed in *Lycosa chaperi* Simon 1885 by Sadana (1972). Anlagen are formed by paired longitudinal invaginations, with the future head of the spermatheca recognizable in early instars by its pores (penultimate anlage, Figs. 4, 5; antepenultimate anlage, Fig. 6.). In the penultimate anlage (Fig. 4) the kidney-shaped vulval chamber is already recognizable.

Structural analysis of the *Sosippus* palp.—The tegulum of the *Sosippus* genital bulb is ring-shaped (see Figs. 7, 9) as in many other lycosoids and agrees in its basic structure with the pisaurid palp (see Sierwald 1990; fig. 2). The sperm duct enters the tegulum dorsally, runs retrolaterally and turns into the ventral section of the tegular ring.

Brady's (1962: fig. 36) figure of a partially inflated *S. californicus* palp labels a median apophysis, conductor, basal haematodocha, lateral apophysis of conductor, mesal apophysis of tegulum, the tegulum, and the embolus. The tegulum appears to carry four conspicuous apophyses labeled here *a*, *b*, *c* and the median apophysis *ma* (Figs. 7, 9). Apophyses *a* and *b* originate from the dorsal section of the tegular ring. Apophysis *a* (labeled conductor by Brady 1962) is long, slender and finger-shaped. At its base it carries a small bilobed fleshy protuberance *p*, which is not visible in the unexpanded bulb. Apophysis *b* (labeled lateral apophysis of conductor by Brady) originates also in the dorsal section of the tegulum next to apophysis *a*. Apophysis *b* is long and sickle-shaped and lies transversely on the ventral surface in the unexpanded bulb. Apophysis *c* (not labeled but figured by Brady 1962 in fig. 36) originates from the ventral section of the bulb as an outgrowth of the tegular wall and is broad and flat. This apophysis is a thin, very translucent, triangular-shaped lamella, which may be difficult to discern under light microscopy. It is unclear at this point if any of these apophyses is a homologue to the pisaurid conductor.

The fourth apophysis arises from the membranous center of the tegular ring and is most likely the homologue of the median apophysis *ma* (labeled mesal apophysis of tegulum by Brady 1962 in fig. 36; the identity of the part he labeled median apophysis is unclear). It is strongly sclerotized; and its dorsal rim is attached to a fringed lamella (Fig. 9), which lies in the notch below protuberance *p* in the non-

inflated bulb (see Dondale 1986, fig. 2). The elongated tips of the sickle-shaped apophysis *b*, the median apophysis and apophysis *c* point in the same direction in the non-inflated bulb, with the tip of the embolus sandwiched between the median apophysis and apophysis *b*.

The section of the tegulum preceding the embolic division becomes very broad and strongly sclerotized (located prolaterally in the non-inflated bulb directly above the lunar plate of the subtegulum, Fig. 7) and corresponds to the distal tegular projection (*dtp*) in the pisaurid palp. The embolic division is connected to the tegulum by a rather narrow, mostly membranous stalk. In the unexpanded palp, this stalk is bent dorsally and retrolaterally, bringing the embolic division over the tegulum, with the tip of the embolus pointing prolaterally. The base of the embolic division is a wide sac, its walls consisting of partially sclerotized and partially membranous sections. The location of this large sac in the embolic division indicates that it is most likely homologous to the basal membranous tube and the distal sclerotized tube of the pisaurid bulb (see Sierwald 1990: fig. 3) and to the palea of other lycosids (labeled palea region (*pr*) in Figs. 7, 9). The embolus is spine-like, thin, curved and rather short, describing an incomplete loop. In *Sosippus* the embolic division carries no apophyses as they occur in other lycosids.

This study confirms the presence of the median apophysis in the *Sosippus* palp as it has been proposed for the Araneoclada (see Codrington 1990: 10; Sierwald 1990: 44). However, the status of the "conductor" in the *Sosippus* palp is unclear at this point. The conductor, as an outgrowth of the tegular wall, can be found in various families of the Araneoclada (e.g., Anyphaenidae, Pisauridae, Amaurobiidae, Psecridae, Araneidae and others). In the *Sosippus* palp, there are three tegular outgrowths (apophyses *a*, *b*, and *c*), each of which may represent the homologue of the Araneoclada conductor. The other two then represent evolutionary novelties.

The long finger-shaped apophysis *a* is shared by all members of the genus and represents a synapomorphy for *Sosippus* (see Brady 1962, figs. 34–47). Figures of the male palp of *Hippasella nitida* Mello-Leitão 1944 (Capocasale 1990: figs. 12, 13, Mello-Leitão 1944, fig. 32) indicate that this species does

not possess the finger-shaped apophysis, and as far as the figures can be interpreted, its palps have no close similarity with the *Sosippus* palp in general. In addition, Mello-Leitão's description (1944: 343) of the size ratio of the eyes (anterior eyes larger than posterior eyes in *H. nitida*) exclude this species from the genus *Sosippus* (posterior median eyes distinctly larger than anterior eyes in *Sosippus*).

Sosippus shares characters with *Porrmosa* Roewer 1960 (Brady 1962, fig. 33; Capocasa 1982, figs. 6–10). The embolic division is similar, consisting of a sac tilted dorsally and retrolaterally and a short, spine-like embolus, whose tip is sandwiched between the strongly sclerotized apophysis *b* and the tip of the median apophysis in the unexpanded palp. The median apophysis is smaller and less strongly sclerotized in *Porrmosa* than in *Sosippus*. Apophysis *a* is present, but it is short, broad and forms a hump (not long and finger-like, labeled conductor in Capocasa 1982, figs. 6–10). Apophysis *c* is represented by a low ridge arising from the ventral section of the tegulum. The shared characters in the palps of both genera support the close relationship of both genera as mentioned by Dondale.

DISCUSSION

Dondale's subfamily proposal forms a valuable starting point for the analysis of the lycosid interrelationship. The characters Dondale employed for his analysis of lycosid subfamilies will require further analyses of the respective palpal structures and additional, independent character systems should be included. According to his proposal the characters "terminal apophysis lost, tegular groove functioning as a conductor," and "embolus laying in a cluster of tegular apophyses" are apomorphies for the *Sosippinae*. Since the sister-group of the *Lycosidae* is not known yet, it is unclear at this point whether the absence of the terminal apophysis in the *Sosippus* palp represents a synapomorphy or is simply the plesiomorphic condition. The present study demonstrates that the "cluster of tegular apophyses" requires further detailed study in other lycosid groups to develop homology hypotheses, especially to clarify the presence or absence of the *Araneoclada* conductor. The character "tegular groove functioning as a

conductor" cannot be evaluated at this point since the actual function of various parts of the palp is unclear (see Zyuzin 1985, 1993 for a detailed discussion). The character "palea developed," the putative key apomorphy for the taxon *Venoniinae-Allocosinae-Pardosinae-Lycosinae*, equally requires further refinement, since it was demonstrated here that the large membranous sac at the base of the embolus in *Sosippus* consists of sclerotized and membranous parts with similarity to the developed palea in other lycosids. A detailed study of the palea morphology will provide further insight into this putative key apomorphy for other lycosid groups.

ACKNOWLEDGMENTS

I wish to thank Dr. M. Deyrup (Archbold Biological Station, Florida) for the *Sosippus* specimens. Preserved material for this study was kindly loaned by Dr. J. Coddington and Scott Larcher (National Museum of Natural History, Washington, DC; USNM), Dr. H.W. Levi (Museum of Comparative Zoology, Cambridge; MCZC), Dr. Norman I. Platnick (American Museum of Natural History, New York; AMNH), and Dr. C.E. Griswold (California Academy of Sciences; CASC). The SEM laboratories of the National Museum of Natural History (Washington, DC) and The Field Museum provided the use of their facilities. I am grateful to Drs. Bennett, Dondale, Stratton, Coddington and an anonymous reviewer for their candid comments on earlier drafts of this manuscript. This study was funded in part by a German Science Foundation grant to the author. Mr. Tariq Farooqui, an undergraduate student from North Park College, Illinois, collected the descriptive data on the males of *Sosippus placidus*. His participation was made possible through an NSF-Internship grant to the Field Museum (DEB93-17449).

LITERATURE CITED

- Brady, A.R. 1962. The spider genus *Sosippus* in North America, Mexico, and Central America (Araneae, Lycosidae). *Psyche*, 69(3):129–164.
 Brady, A.R. 1972. Geographic variation and speciation in the *Sosippus floridanus* species group (Araneae: Lycosidae). *Psyche*, 79(1/2):27–47.
 Brignoli, P.M. 1983. A Catalogue of the Araneae, Described Between 1940 and 1981. Manchester Univ. Press. 755 pp.
 Capocasa, R.M. 1982. Las especies del genero

- Porrmosa* Roewer, 1959 (Araneae, Hippasinae). *J. Arachnol.*, 10:145–156.
- Capocasale, R.M. 1990. Las especies de la subfamilia Hippasinae de America del Sur (Araneae, Lycosidae). *J. Arachnol.*, 18:131–141.
- Coddington, J.A. 1990. Ontogeny and homology in the male palpus of orb-weaving spiders and their relatives, with comments on phylogeny (Araneoclauda: Araneoidea, Deinopoidea). *Smithsonian Contr. Zool.*, 496:1–52.
- Coddington, J.A. & H.W. Levi. 1991. Systematics and the evolution of spiders (Araneae). *Ann. Rev. Ecol. Syst.*, 22:565–592.
- Dept. of the Interior, US Fish and Wildlife Service. 1994. Endangered and threatened wildlife and plants; animal candidate review. 50 CFR Part 17. *Federal Register*, 59(219):58982–59028.
- Dept. of the Interior, US Fish and Wildlife Service. 1995. Endangered and threatened wildlife and plants. 50 CFR Part 17. *Federal Register*, 61(28): Candidate categories review –candidate taxa reclassification 7457–7463; plant and animal taxa: 7596–7613.
- Dondale, C.D. 1986. The subfamilies of wolf spiders (Araneae: Lycosidae): Pp. 327–332, *In Actas X Congreso Internacional de Aracnologia* (J.A. Barrientos, ed.). Jaca, Spain.
- Gertsch, W.J. 1949. *American Spiders*. D. van Nostrand Co., Torontot, New York, London. 285 pp.
- Griswold, C.E. 1993. Investigations into the phylogeny of the lycosoid spiders and their kin (Arachnida, Araneae, Lycosoidea). *Smithsonian Contr. Zool.*, 539:1–39.
- Lachmuth, U., M. Grasshoff & F.G. Barth. 1985. Taxonomische Revision der Gattung *Cupiennius* Simon 1891 (Arachnida: Araneae: Ctenidae). *Senck. Biol.*, 65(3/6):329–372.
- Lehtinen, P. & H. Hippa. 1979. Spiders of the Oriental-Australian Region. I. Lycosidae: Venoniinae and Zoicinae. *Ann. Zool. Fennici*, 16:1–22.
- Mello-Leitão, C. 1944. Arañas de la Provincia de Buenos Aires. *Rev. Mus. La Plata (N.S.) (Zool.)*, 3(24):311–393.
- Roewer, C.-F. 1959. Araneae Lycosaeformia IIa. Lycosidae: 1–518. *Exploration du Parc National de l'Upemba*, Mission G.F. de Witte. Bruxelles.
- Sadana, G.L. 1972. Studies on the postembryonic development of the epigynum of *Lycosa chaperi* Simon (Lycosidae: Araneida). *Research Bulletin, Panjab University*, 23(3/4):243–247.
- Sierwald, P. 1989. Morphology and ontogeny of female copulatory organs in American Pisauridae, with special reference to homologous features (Arachnida: Araneae). *Smithsonian Contr. Zool.*, 484:1–24.
- Sierwald, P. 1990. Morphology and homological features in the male palpal organ in Pisauridae and other spider families, with notes on the taxonomy of Pisauridae (Arachnida: Araneae). *Nemouria*, 35:1–59.
- Simon, E. 1888. Descriptions d'espèces et de genres nouveaux de l'Amérique centrale et des Antilles. *Ann. Soc. Entomol. France*, 8(6):203–216.
- Simon, E. 1898. *Histoire Naturelle des Araignées*. Roret, Paris 2(2):193–380.
- Zyuzin, A.A. 1985. [Generic and subfamilial criteria in the systematics of the spider family Lycosidae (Aranei), with the description of a new genus and two new subfamilies]. *Proc. Zool. Inst., Leningrad*, 139:40–51 [in Russian].
- Zyuzin, A.A. 1993. Studies on the wolf spiders (Araneae: Lycosidae). I. A new genus and species from Kazakhstan, with comments on the Lycosinae. *Mem. Queensland Mus.*, 33(2):693–700.

Manuscript received 6 July 1999, revised 18 January 2000.